Faunal influence on sediment stability in intertidal mudflats

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Chapter 3

Vertical migration of nematodes and harpacticoids in tidal flats

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Introduction

Organisms living in the surficial layers of intertidal sediments are exposed to extreme fluctuations in the chemical and physical environment caused by the tidal, diurnal and seasonal cycles. Vertical migration, up and down the sediment, driven by factors such as moisture content, oxygen concentration or food availability, is one way in which they may adapt to their changing environment.

Whereas the behavioural responses of large macrofaunal organisms to tidal fluctuations are easily discernible, only a few studies have addressed the potential migration on a tidal time scale of the smaller meiobenthos. In intertidal studies one often investigates one vertical profile per site and it is tacitly assumed that temporal variation caused by the tides may be ignored (Soetaert et al., 1994). However, the validity of this assumption remains to be tested. Boaden and Platt (1971) showed in a study from a beach in South Bay, Northern Ireland, that nematodes, an important component of intertidal meiobenthos, did generally not migrate, except when water flooded the sampling area. This provoked downward movement of the animals, a result confirmed later by experiments of Palmer & Molloy (1986) and Fegley (1987), showing downward migration of nematodes as a reaction to increased current speeds. Steyaert et al. (2001) showed that the migration pattern differs between species. Upward migration during inundation was suggested for harpacticoids in a study by Joint et al. (1982). All these studies concern sandy intertidal areas. Migration in fine grained intertidal sediments is as yet undocumented.

Several meiobenthic studies have dealt with vertical distribution patterns and related these to the biogeochemical characteristics of the sediment (Vanreusel et al., 1995; Soetaert et al., 1997; Vanhove et al., 1998). Hendelberg & Jensen (1993) observed a significant seasonal shift in vertical distribution of nematodes that was triggered by oxygen deficiency and sulphide stress in a muddy sheltered bay.

We studied the fine-scale migration patterns of nematodes and harpacticoids in intertidal flats of three estuaries. In the Dollard and Eden estuary, the vertical distribution of these organisms in the top centimetres of the sediment was followed while the flats were exposed; grain-size, and on one occasion chlorophyll *a* distribution were also determined. In the Westerschelde, the vertical distributions of the fauna during ebb and flood tides were compared.

Material and methods

Sampling sites

Vertical patterns of the meiobenthos were studied in three intertidal flats in the Westerschelde (the Netherlands), Eden (U.K.) and Dollard estuaries (the Netherlands) in April 1994, April 1996 and August 1995, respectively. The sampling site in the Westerschelde estuary (WO22) was located in the eastern part (4°01'56" E and 51°24'21" N), the site in the Eden estuary was situated at the northwestern shore (2°53'01" W and 56°21'59" N) and the Dollard site was situated in the middle of the estuary at the edge of the intertidal flat 'Heringplaat' (7°09'20" E and 53°17'10" N). All three field sites are located in relatively sheltered areas. The main disturbance of the sediment occurs when wind induced waves cross the sites. The salinity at all three sites varied around 15 PSU.

Sampling strategy

Meiobenthos was sampled with tube corers with an internal diameter of 3.6 cm and a length of 30 cm. The cores were sliced immediately in the field, with the help of a piston-corer as described by Joint et al. (1982). The meiobenthic samples were fixed with 4% borax-buffered formaldehyde solution and stored in the dark.

Meiobenthos recovery as a function of slice thickness was tested during the first sampling campaign in the Westerschelde estuary, to see whether the sampling device could be used to compare vertical distributions of inundated and exposed fine-grained sediments. Nine replicate cores were taken within a quadrate of 4 m^2 when the flat had been exposed for almost three hours and nine cores were taken in the same quadrate when the sampling site was covered with 30 centimetre of water. The top two centimetres of three cores at the two sampling times were sliced into 2.5 mm thick layers, three cores were subdivided into four layers of 5 mm and three cores into two layers of 10 mm. The total number of meiobenthos individuals in the top two centimetre of the sediment of the nine cores was compared. The effect of the thickness of slicing on the total amount of individuals found was tested using ANCOVA with the tide as covariate.

The vertical distribution during exposure of the mudflats in the Dollard and Eden estuary was studied in five 2 mm slices in the top centimetre of the sediment, two 5 mm slices in the 1-2 cm layer and one 30 mm slice extending till 5 centimetre deep. One core was taken every half hour in a plot of 4 m^2 during a period of 6 hours in the Dollard estuary. We choose for this temporal replication above real replication, because slicing replicates immediately was not possible, so migration could occur when a replicate core was waiting to be sliced. The first core was taken as soon as the flat was exposed, the last two cores were taken at water depths of 0.5 and 25 centimetre respectively. The sampling station in the Eden estuary was sampled four and three times during exposure on two different days.

Additional cores were taken in the Westerschelde and Dollard estuary to measure grain size distribution. In the Dollard estuary, chlorophyll *a* distribution was also studied in the same sampling plot, at the same time as the meiobenthos, and oxygen profiles were measured with a micro-electrode.

Analysis

The meiobenthos was extracted from the sediment by a density centrifugation technique with the colloidal silica gel ludox HS40 (Heip et al., 1985). Nematodes and harpacticoids, the main constituents of the meiobenthos, were counted. In the Westerschelde site, the other meiobenthic taxa were counted as well. Grain size was measured with a Malvern particle analyser 3600 EC and chlorophyll *a* was analysed according to Lorenzen (1967).

Log linear models were used to test whether there was a significant change of the vertical distribution of nematodes and harpacticoids over time (Sokal & Rohlf, 1995). Within these models, an estimation is made of the vertical distribution at a certain moment based on the observed number at each moment in each layer. Subsequently the difference between estimated and observed profiles is tested.

Results

Sediment

Sediments from the Westerschelde site consisted mainly of silt (55%). The upper 2 centimetres were muddier (median grain size of 45 µm) than the sediment deeper down (median grain size of 70 µm). The sediment at the Dollard site had a median grain size of 78 µm and a silt content of 38%. Sediments at the Eden estuary site had a median grain size of 110 µm (Black & Paterson, pers. comm.).

Chlorophyll *a* conctent peaked at the surface (0-2 mm.) of the sediment at the Dollard site. The content in the surface layer was about 12.5 µg g^{-1} dry sediment at the beginning of the sampling period. This increased to ± 16 µg g^{-1} dry sediment. There was also a small increase in the subsurface layer (2-4 mm.). The content in the rest of the two centimetres varied between 8.5 and 10.5 µg g^{-1} dry weight sediment.

Oxygen penetration increased during exposure at the Dollard site from about one mm during flood to about 4 mm during exposure. Because of the high mud content the sediments retained their moisture level during the entire ebb phase at all sites.

Table 3.1. Mean (± standard error) number of meiobenthos and nematodes per 10 cm^2 in the top two centimetres of the sediment in the Westerschelde estuary, using different slice thicknesses, at two moments during a tidal cycle: 9:00 h when the flat is exposed and 14:00 h when flood is in and the sampling site is covered with 30 centimetre of water.

time (h)	Slice thickness (mm)	total meiobenthos	Nematodes
09:00	10	1511 (540)	1243 (410)
09:00	5	1509 (460)	1294 (271)
09:00	2.5	1066 (498)	797 (171)
14:00	10	1264 (342)	1003 (215)
14:00	5	975 (121)	775 (69)
14:00	2.5	1271 (457)	995 (327)

Table 3.2. Total mean (± standard error) numbers of meiobenthos per 10 cm^2 in the top five and in the top two centimetre of the sediment in the Westerschelde estuary. Numbers are the mean, the standard errors are in brackets, n=18.

	Total meiobenthos	Nematodes	Harpacti-coids	Harpacticoid nauplii	Oligo-chaetes	Ostra-cods
5 cm.	1420 (425)	1154 (329)	27 (15)	71 (64)	74 (33)	65 (70)
2 cm.	1283 (435)	1018 (316)	24 (14)	70 (64)	73 (34)	57 (71)

Table 3.3. Mean (± standard error) number of nematodes and harpacticoids per 10 cm^2 in the top two centimetres of the sediments and the percentage relative to the top five centimeter.

Site	Nematodes	%	Harpacticoids	%
Westerschelde	1018 (316)	88	24 (14)	89
Dollard	3145 (628)	82	68 (21)	97
Eden1	2590 (610)	79	221 (94)	97
Eden2	3414 (625)	80	493 (194)	99

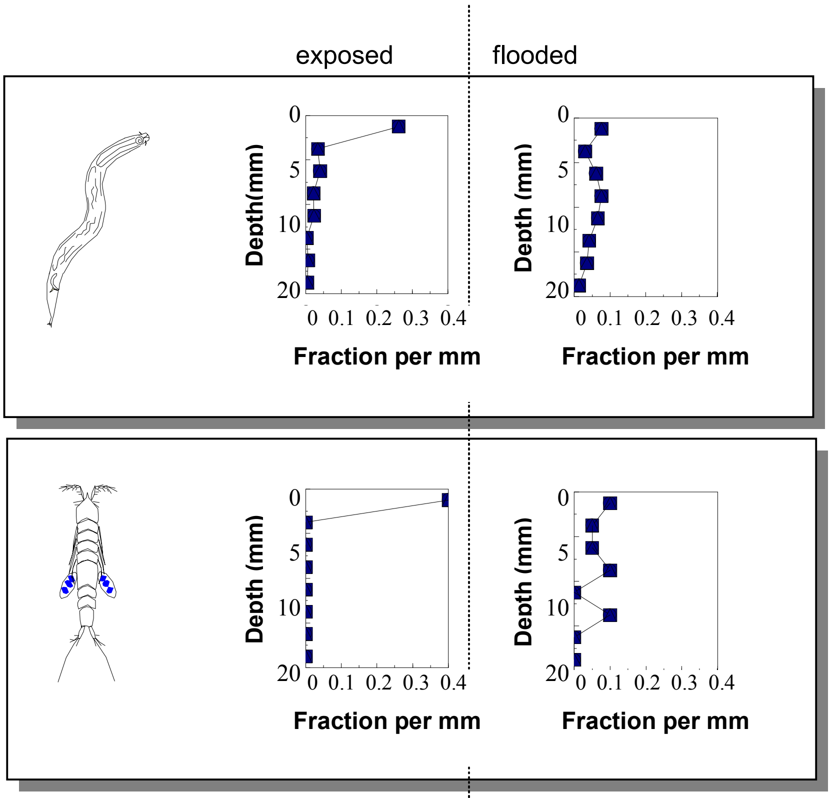

Figure 3.1. The vertical distribution of the nematodes and harpacticoids in the top two centimetres of the sediment at sampling point WO22 in the Westerschelde estuary, at exposed and flooded conditions.

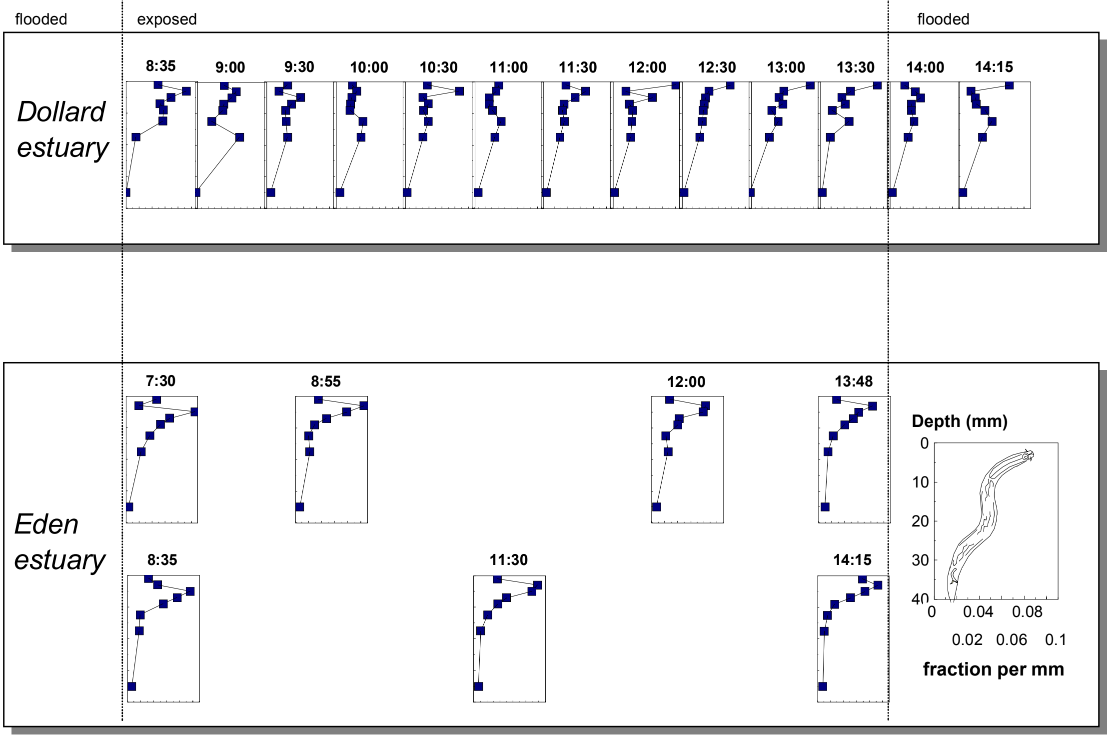

Figure 3.2. The vertical distribution of nematodes in the top five centimetres of the sediment in the Dollard and the Eden estuary. The data of the Eden estuary are from two successive days and the graphs are ordered according to the beginning of exposure. All graphs have the same scale.

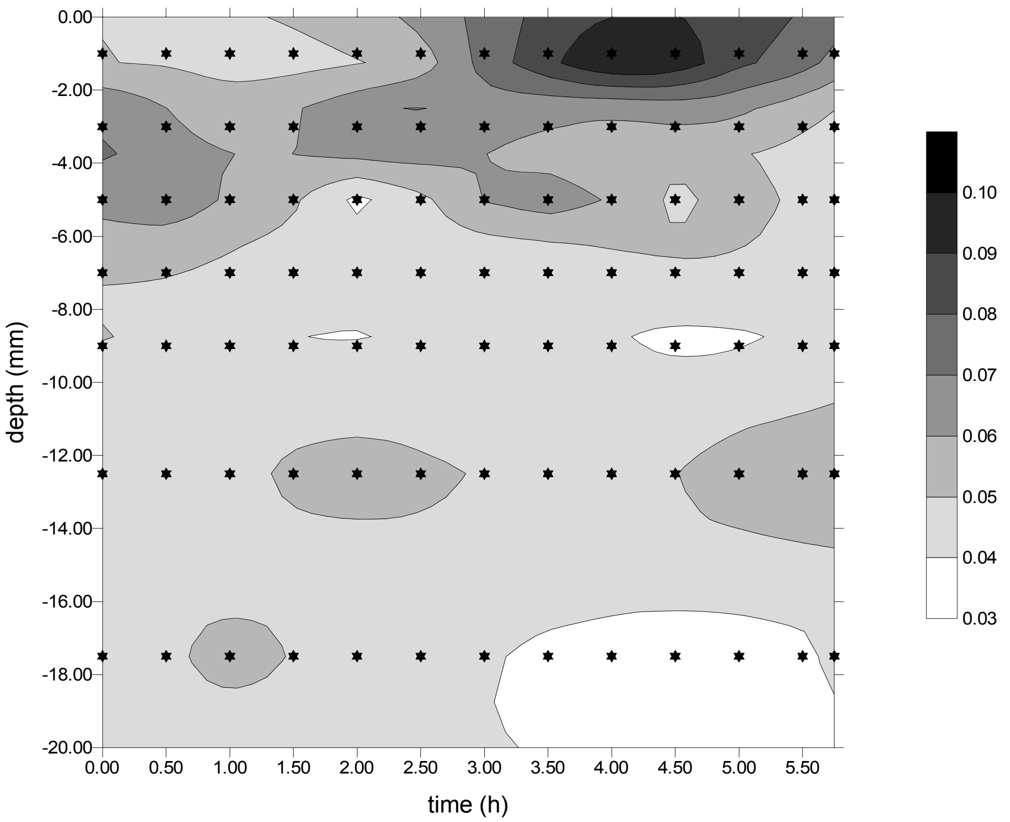

Figure 3.3. Relative abundance of nematodes per millimeter in the top two centimeter of the sediment from the beginning of exposure till 45 minutes after exposure time. The contours were calculated with Kriging.

Meiobenthos

No significant effect of slice thickness was found on the total number of meiobenthic animals and the number of nematodes recovered in the top two centimetres of the Westerschelde site (Table 3.1, ANCOVA, $F_{2,12} = 0.9$; n.s.), so the piston-corer could be used to determine fine-scale distribution patterns of meiobenthos.

The most abundant meiobenthic groups at the sampling site in the Westerschelde estuary were nematodes (82%), oligochaetes (6%), harpacticoid nauplii (5%), ostracods (4%) and adult harpacticoids (2%)(Table 3.2). Nematode densities in the Dollard and in the Eden estuary were almost three times as high as in the Westerschelde. Average densities of respectively 3922 ± 994 and 3755 ± 878 nematodes per 10 cm^2 were found in the top five centimetre of the sediment, against 1154 ± 329 per 10 cm^2 in the Westerschelde estuary. On average, nematodes were 10 times as abundant as the harpacticoids in the Eden estuary, and more than 50 times as abundant in the Dollard estuary (Table 3.3).

Most nematodes, about 80%, were present in the top two centimetres of the Dollard and Eden sediments (Table 3.3). Similarly, about ninety percent of all the Westerschelde meiobenthos or nematodes, was found in the top two centimetres (Table 3.3). The total number of nematodes in the upper two centimetres of the sediment at all three sampling sites did not change significantly (ANCOVA, $F_{1,12}$ = 0.2; n.s.) during the sampling period. No migration into or out of deeper layers or in and out of the water column could be detected.

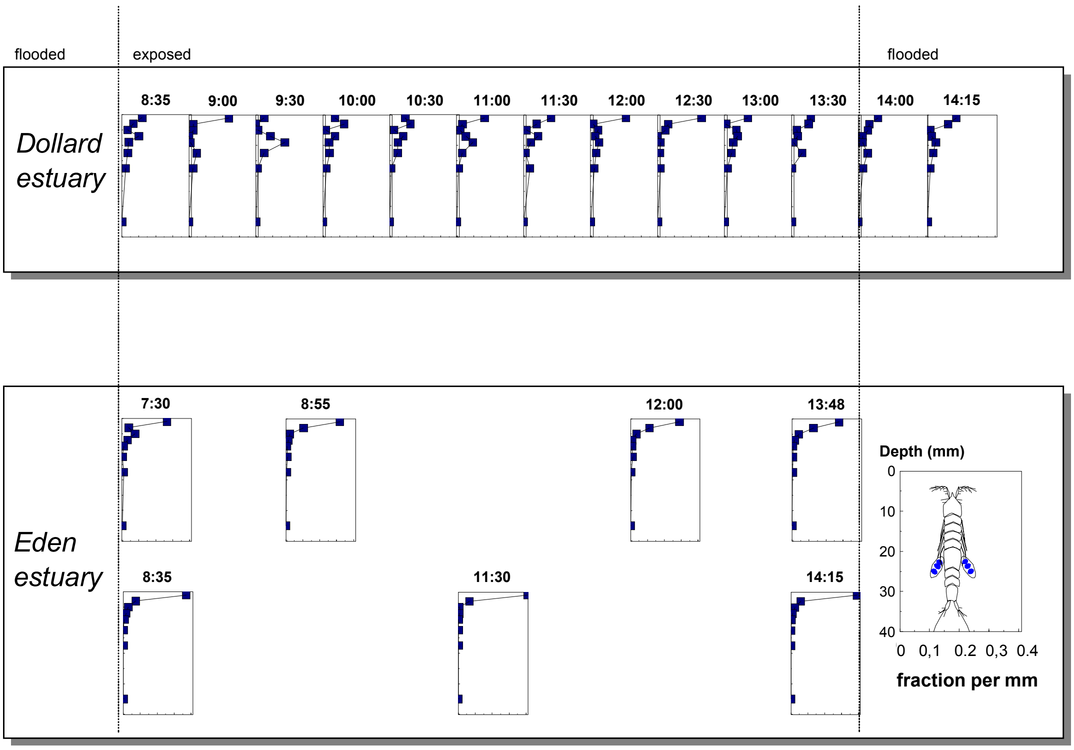

Figure 3.4. The vertical distribution of harpacticoids in the top five centimetres of the sediment in the Dollard and the Eden estuary. The data of the Eden estuary are from two successive days and the graphs are ordered according to the beginning of exposure. Graphs have a different scale.

Fine-scale vertical distribution of nematodes and harpacticoids

Two-way ANOVA indicated that there was a significant difference in the vertical distribution of both nematodes (ANOVA, $F_{7,32} = 7.8$; $p < 0.001$) and harpacticoids (ANOVA, $F_{7,32} = 11.2$; $p < 0.001$) in the Westerschelde between low tide and flood tide (Figure 3.1). About 60 to 100% of the nematodes and harpacticoids were found in the top two millimetres of the sediment when the sampling site had been exposed for three hours. Half an hour after the area was flooded only 20 to 50% were found in the top two millimetres, and there was an increase in abundance of the nematodes and harpacticoids in the underlying layers down to 15 millimetres.

The time series of the Dollard showed a more or less uniform distribution of nematodes in the upper 2 centimetres of the sediment shortly after exposure (8:35 hours, Figure 3.2). This distribution was maintained for about three and a half hours, after which nematodes tended to be more concentrated near the surface (12:00 till 13:30)(Figure 3.3). The relative dominance of nematodes in the upper two mm was 8 ± 1%, during the first period of exposure (8.35 to 11:30) and 18 ± 2 % during the second half (12:00 to 13:30). Nematode density near the surface decreased as soon as water covered the field site (14:00 hours Figure 3.3). Log linear models (Sokal & Rohlf, 1995) confirmed that there was a significant change in vertical distribution of the nematodes during exposure time. There was no significant effect for the harpacticoids, and the vertical distribution pattern was irregular during the sampling period (Figure 3.4). The density seemed to reach a maximum in the surface millimetres three to four hours after the site was exposed.

The results of the Eden estuary similarly demonstrate a tendency for nematodes to become more concentrated towards the surface with exposure time (Figure 3.2). Peak abundance of nematodes was found three millimetres deep in the sediment when water crossed the sampling sites. Harpacticoid copepods were concentrated towards the surface during the entire period of exposure (Figure 3.4).

Discussion

Nematodes comprise 80 to 95% of the meiobenthos in mudflats (Heip et al., 1985), copepods usually are subdominant (Giere, 1993). This pattern was confirmed in our study where nematodes far outnumbered harpacticoid copepods; in the Westerschelde station they accounted for 82% of the meiobenthic individuals. The nematode densities at our three field sites, varied between 900 (Westerschelde) and 4000 individuals 10 cm^{-2} (Eden, Dollard), which falls well within ranges reported from European estuaries (Soetaert et al., 1995).

The vertical distribution of nematodes in the sediment was distinctly different between the three sampling sites. During exposure, some 60 to 80% of all nematodes in the Westerschelde site resided in the upper 2.5 mm of the sediment (Figure 3.1). In the Dollard site, the relative density in the upper 2 mm was at most 20 %, observed at one sampling event at the end of the ebb phase (13:30 in Figure 3.2). The vertical distribution in the Eden site was consistently characterised by a well-demarcated subsurface peak, at 3-5 mm depth; relative densities in the upper 2 mm never exceeded 14 % (Figure 3.2). Similar discrepancies between sites were observed at the onset of submergence, with surface dominance of 20-50% in the Westerschelde site (Figure 3.1) and 5-15% in the Dollard site (Figure 3.2). On average only 10% of the nematodes was found below 2 centimetres depth in the Westerschelde site, about 20

% in the other two sites. Harpacticoids tended to reside near the surface during exposure in all three estuaries, but in the Dollard a subsurface peak was discernible on certain occasions.

Of all three sediments, the one from the Westerschelde was the most muddy, followed by the Dollard, and finally the Eden sediment. As such the differences between the sites (for nematodes) are consistent with the notion that the meiobenthos in muddy sediments is more restricted to the surface layers than in more sandy sediments (Arlt, 1973; Vanhove et al., 1998). The nematode/harpacticoid ratio decreased with increasing grain size as described by Raffaelli & Mason (1981) and in the Eden estuary, the high densities of harpacticoid copepods in the upper section of the sediment may well have contributed to the reduced densities of nematodes there.

In addition to station-specific effects, the changing abiotic conditions caused by the tides as well as small-scale horizontal variation may impact the vertical pattern. The effect of spatial compared to temporal heterogeneity was addressed in the samples from the Westerschelde estuary where three replicates taken at ebb and flood were compared. There was a significant difference between the vertical distribution of the nematodes and harpacticoids at the two sampling periods, indicating that temporal changes were dominant compared to small-scale spatial differences. Therefore we processed only one replicate for our subsequent analysis of the patterns in the other estuaries, but with a shorter time interval especially in the Dollard.

In the Westerschelde site, nematodes and harpacticoids were significantly more abundant near the sediment surface when the sediment was exposed for three hours than when the sediment was covered by 30 cm of water. Such differences were also described by Boaden and Platt (1971) who found a rapid downward migration of nematodes in cores, sliced in centimetre layers, as soon as the tide crossed their field site. In addition, flume experiments have demonstrated that nematodes migrated some 2 to 15 mm down whereas harpacticoids stayed near the surface when flow increased (Palmer & Gust, 1985); and similar patterns were observed in the field by Warwick & Gee (1984) and Fegley (1987). Steyaert et al. (2001) found in sandy sediments in the Westerschelde also less nematodes in the top sediment layers during submersion, but some species were more abundant in the surface layer than during exposure. This indicates that the migration pattern depends on the species. The abrupt change in the vertical distribution pattern of nematodes in the Dollard site at the onset of flood (compare the distribution at 13:30 and 14:00 hours in Figure 3.2) further indicates such a sudden downward retreat although its significance cannot be tested. The downward migration can be either a protection against erosion or against predation (Coull et al., 1989).

In the Dollard site and in the Eden estuary (2^{nd} sampling period), nematodes were more concentrated towards the sediment surface at the end of the ebb phase than at the onset of exposure. Although this result was significant for the Dollard estuary, the differences were small and indicative of net movement over the scale of millimetres only. Harpacticoid copepods did not exhibit the same consistent behaviour.

Because the net movements are restricted to such small ranges and as the details of the abiotic fators at similar resolution are lacking, we can only speculate about their causes. It has been suggested that nematodes and harpacticoids move in response to light intensity, temperature, water content, oxygen penetration, physical disturbance, food distribution (Boaden & Platt, 1971; McIntyre, 1969; Montagna et al., 1989; Moodley et al., 1998; Palmer & Gust, 1985; Rudnick et al., 1985), species interaction (Joint et al., 1982), macrobenthic activity or a combination of some of these factors. If we proceed from the downward retreat at the onset of flood, then nearly all of these factors can be responsible for the gradual recovery of a more surficial distribution during exposure.

The fact that net vertical displacement is hardly discernable in all estuaries does not imply that nematodes and harpacticoids remain stationary. Probably the animals move over much larger distances, horizontal and vertical. If we want to assess the possible impact of these small animals on the sediment (Aller & Aller, 1992), it is this gross movement, not the net effect of it that we may need to quantify.

To conclude we have demonstrated that there are subtle, tidally induced changes in the way nematodes and, to a lesser extent, harpacticoid copepods are distributed in muddy sediments. Although these temporal effects may predominate over small-scale spatial effects, they are only minor compared to differences existing between different sites. Therefore, if we want to understand the factors that determine meiobenthic vertical distribution in intertidal areas, it may be opportune to concentrate efforts to sampling an array of different sites rather than to focus on temporal differences at any one site, or to experimentally manipulate the factors thought to be responsible.